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The formation of waves is a vivid example of collective behaviour occurring in insects, birds, fish and mammals, which has been interpreted as an antipredator response. In birds a quantitative characterization of this phenomenon, involving thousands of individuals, is missing and its link with predation remains elusive. We studied waves in flocks of starlings, a highly gregarious species, by both direct observation and quantitative computer vision analysis of HD video recordings, under predation by peregrine falcons, *Falco peregrinus*. We found that waves originated from the position of the attacking predator and always propagated away from it. We measured their frequency and velocities, the latter often being larger than the velocity of the flock. A high positive correlation was found between the formation of waves and reduced predation success. We suggest that the tendency of a prey to escape, when initiated even by a few individuals in a cohesive group, elicits self-organized density waves. Such evident fluctuations in the local structure of the flocks are efficient in confusing predators.

The formation of waves is a vivid example of self-organized collective behaviour occurring in insect swarms, bird flocks, fish schools and mammalian herds (Krause & Ruxton 2002; Couzin & Krause 2003; Gerlotto et al. 2006; Kastberger et al. 2008). Several authors have described such waves as (1) a collective response possibly facilitating cohesion in the presence of a predator, (2) rapid reorganization of a group upon predator attacks and (3) rapid information transfer within a large group (Radakov 1973; Webb 1980; Treherne & Foster 1981; Gerlotto et al. 2006).

Where a predator approaches a group of prey, those nearest the predator become aware of it first and react, for example by alarm call or acceleration, thereby alerting other members of the group otherwise unaware of the threat. If the rate of transmission of this information is faster than the predator's speed of approach, individuals on the far side of the group will be alerted earlier than if they were alone. In water insects and fish this phenomenon has been labelled the 'Trafalgar effect' because of the signals that were sent between ships to Admiral Nelson before the battle of Trafalgar informing him that the French and Spanish combined fleet was leaving Cadiz, even though it was below the horizon of his flagship, HMS Victory (Caro 2005). Treherne & Foster (1981), who coined this term, showed that marine isopods, *Halobates robustus*, increased velocity in response to a model predator and this change of motion spread across the group faster than the speed of approach of the predator. The same hypothesis has been suggested for flocking birds under predation risk (Heppner 1997; Michaelsen & Byrkjedal 2002; Caro 2005). In particular, in flocking dunlins, *Calidris alpina*, an accelerating wave has been described, reaching a speed three times higher than would be possible if birds were reacting only to the nearest neighbours, in an organization similar to a human chorus line in which individuals observe the approaching wave and time their own performance to coincide with its arrival (Potts 1984).

It could be that waves represent a peculiar form of 'mobbing', which occurs when individuals of certain species mob a predator by

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cooperatively harassing it, in order to scare it (Krause & Ruxton 2002). If this were the case, waves would be expected to move towards the predator. Another hypothesis is that wave activity, by means of a local breaking of the spatial order of the group, can confuse the attacking predator, thereby reducing its chance of success (Treherne & Foster 1981; Buchanan et al. 1988; Kastberger et al. 2008).

Few systematic observations, or quantitative and qualitative descriptions, of waves in bird flocks have been made. It is therefore relevant to carry out detailed characterization studies to understand their mechanism(s) of formation and ultimate functions as well as to provide empirical data for individual-based models of collective behaviours. The European starling is an extremely gregarious bird species that forms flocks of thousands of individuals during autumn and winter (Feare 1984). In starlings, a commonly observed aerial collective behaviour results from waves that can be detected from a great distance. Although this phenomenon has been described anecdotally and is thought to occur in relation to aerial predation by falcons (Tinbergen 1951; Feare 1984), its mechanism and function remain largely unknown. In this study, we quantified the occurrence of propagating waves and their relation to predation.

In the following, we refer to a wave event (WE), which we define as a train of several observable pulses of optical intensity that propagates along a given direction across the flock, not preceded and not followed by any other train for at least 10 s. Our aim in this study was to investigate (1) the circumstances under which a WE occurs; (2) the correlation between waves and the success of the predator; (3) the wave's direction of propagation; (4) the correlation between predator position and origin of the wave; and (5) the frequency and speed of propagation of the waves. We first focus on the whole WE and on its links to predation, and then on the propagation of single pulses.

METHODS

Field Video Recording

Data were collected from flying flocks of European starlings in proximity to two winter urban roosts in Rome, Italy (41°44′N–12°24′E), situated 10 km from each other. Between 14 January 2006 and 17 March 2006 we carried out 53 video-recording sessions, and between 12 December 2006 and 2 March 2007 57 video-recording sessions, in parallel with behavioural observations. One roost is located in the city centre (Termini), it comprises approximately 20 000 birds and has been used for at least 50 years; the other roost is located in the southern part of the city (EUR), with about 60 000 birds roosting daily, and it has been in use for about 20 years.

Flocks were videotaped from a fixed location (roof of a building for roost Termini; open field for roost EUR; the distance from the birds ranged from 200 m to 500–1000 m) with the operators being in place about 90 min before sunset (when the first flocks arrive), until darkness. Opportunistic video recording was carried out with a High Definition video camera (JY-HD10, JVC, 30 fps) on miniDV digital tapes. These video recordings were specifically aimed at the aerial displays of the flocks above the roost before and during landing when a predator was actively hunting, eliciting visible collective responses. Peregrine falcons, *Falco peregrinus*, frequently attack the incoming flocks in both roosts (Carere et al. 2009: Zoratto et al. 2010). During the first winter sessions they were observed in 31 of 53 observation sessions at the roosts, whereas during the second winter sessions they were observed in 50 of 57. In both winters, attacks came from two individuals in Termini and up to five individuals in EUR. We successfully videotaped more than 100 wave events, from which we selected those that matched the requirements for frame processing (see below and the video clips in the Supplementary Material) and that were recorded on days with stable atmospheric conditions, especially wind speed [wind intensity was limited to a range of 0–4 (Beaufort scale)], and with high visibility.

Field Observations

From 12 December 2006 to 2 March 2007 we performed behavioural observations at the roosts for a total of 16 days in Termini and 41 days in EUR. Hunting falcons were observed during 10 days in Termini and 40 days in EUR. On these days we recorded the number of all hunting sequences (HSs) occurring at the roosts, where a single HS is defined as the whole set of manoeuvres adopted by one or more attacking predators against the same flock. A sequence started when at least one falcon approached a flock and stopped when the falcon caught a starling (successful sequence) or when it withdrew from one flock, either disappearing or moving to another flock (unsuccessful sequence). This definition is equivalent to the term 'hunt' used for the first time by Rudebeck (1951) and more recently by Dekker (2003) and to the term 'attack' used by Cresswell (1996). For each HS we also recorded its duration and the number of attacks. Within each HS we recorded the number of WEs; each observed WE (occurring in the presence of the predator in close proximity to the flock) was characterized by the direction of propagation of the wave front with respect to the position of the falcon.

We note that, as mentioned by other authors, any rigid rotation of a flock can result in a fast wave that is just an optical illusion because of a sort of interference resembling 'moiré patterns' (Davis 1980; Heppner 1997). In such a scenario, the WEs that we filmed would be just signals without any information transfer, that is, without biological meaning. Technically, identifying and quantifying such an effect is a very demanding task. Even so, in the WEs that we analysed we can reasonably exclude the presence of similar illusions by direct observations from the field: we firmly believe that such experience leaves no doubt to the density nature of starlings' waves and their causal interaction with the predator.

Statistical Analyses of the Observations

For all the quantitative variables from the field observations we used both parametric and nonparametric tests. For variables with three or more levels, we used analysis of variance (parametric ANOVA) with a completely randomized design (one between-subjects factor) and a Kruskal–Wallis test. For variables with two levels we used Student *t* tests for independent groups (both homogeneous and nonhomogeneous variances) and a Mann–Whitney test. A Levene test for variance homogeneity was conducted in all cases prior to the analysis. For categorical (or categorized) variables we used a chi-square test for variables with three or more levels and a Fisher's exact test for variables with two levels.

Video Processing and Measurements of Frequency and Velocity

Each movie, in mpeg2 format, was converted into frames, JPEG format (1280 × 720), with the software HiMovie HD (package HiLife, Apple). We computed the frequencies of 21 WEs: these were selected because of their particularly clear optical flow, which allowed us to follow the waves along their propagation. To measure frequency, two of us (A.P. and C.C.) independently counted the waves composing a WE, in a given temporal boundary, in both normal and slow motion. The measurements agreed perfectly between observers (Appendix Table A1).

To retrieve information on velocity, the images were processed with an in-house-built program using LTI libraries (http://ltilib.sourceforge.net/doc/homepage/index.shtml), which transforms

them into intensity channels. Our method is based on the correspondence between the density variation and the optical flow of the light intensity. Any image was filtered by isolating the flock, removing the background and producing a 'negative' of the original image, where the intensity of the densest region was normalized to a value of 1 on a scale of [0:1]. With a threshold T_F, set empirically at about 0.5, the brightest part was selected, the result was smoothed for noise reduction and then finally processed with a segmentation algorithm (performed by the class lti::objectsFromMask of LTI libraries), which identified the cluster representing the flock and its centre of area (**F** = centre of the flock). This operation transformed the original frames into a sequence of channels, each one entirely set to black except for the part included within the border of the flock (Fig. 1). A second threshold (T_P) was then applied to the main cluster to select the densest region, which corresponds to the wave pulse, and identify the centre of its area (**P** = centre of the wave pulse).

The estimation of the relative velocity proceeded as follows.

(1) The two-dimensional difference vector $\mathbf{D}(T_F,T_P) = \mathbf{P}(T_P) - \mathbf{F}(T_F)$ represents the position of the wave pulse in the reference frame of the flock. This vector can be considered as a function of T_P only since the uncertainty on it is dominated by the uncertainty on the determination of $\mathbf{P}(T_P)$. In the Appendix, the same argument is applied directly to L^p as defined below. Vector $\mathbf{D}(T_P)$ was used to study the dynamics of the wave: each frame is associated with an instance of $\mathbf{D}(T_P)$.

(2) The discrete trajectory underwent a standard smoothing process: a Gaussian b-spline was computed from the vertices of $\mathbf{D}(T_P)$. Such interpolation represents the instant position of **P** (the centre of the small blue cluster in Fig. 1), with respect to **F** (the large red cluster in Fig. 1). The length in pixels of the trajectory related to a particular value of T_P was calculated as the length of the splined trajectory and called $L^p(T_P)$.

(3) To reduce the noise, the final length L^p was then obtained as an average on T_P, over an interval of values (as described in the Appendix).

(4) To convert this length L^p into a metric distance, L^m, we used as a fixed reference the dimensions of the attacking peregrine falcon, according to commonly accepted morphometric measurements: 36–48 cm for length; 95–110 cm for wing span (Cramp & Perrins 1994).

(5) The conversion formula derived from elementary optics is

$$L^m = L^p \times A^m / a^p \quad (1)$$

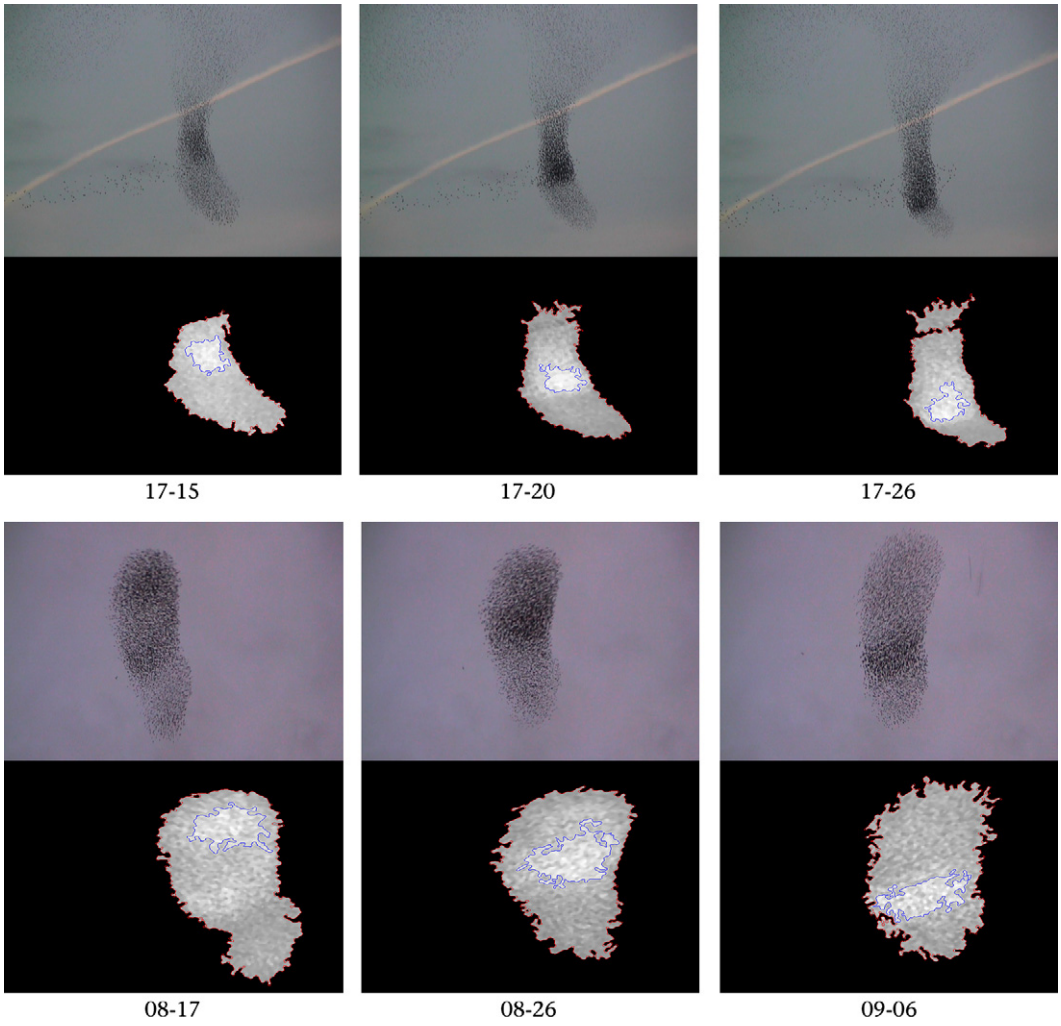

Figure 1. Analysis of wave pulses: computer vision analysis of wave pulses propagating across two different flocks (estimated velocities: 25.24 m/s and 13.73 m/s, video clip no. 7 in the Supplementary Material). Below the original video frame, the digital segmentation of both the flock (red contour) and the pulse within the flock (blue contour) is shown. Cameras captured 30 frames/s; each frame is labelled with time (s) and frame number (for details see Methods; for more examples see the video clips in the Supplementary Material).

Table 1
Relative velocity of single wave pulses estimated in 15 wave events

Wave event	Total frames	Duration (s)	Velocity (m/s)	Error (m/s)
Series 1a	10	0.33	15.56	1.52
Series 1b	27	0.90	6.89	0.49
Series 4	12	0.40	25.24	4.21
Series 8a	31	1.033	17.47	1.35
Series 8b	11	0.37	25.10	2.06
Series 8c	17	0.57	13.73	1.10
Series 8d	37	1.23	7.79	0.62
Series 9	22	0.73	18.26	3.04
Series 10	57	1.90	7.63	0.54
Series 12	15	0.50	9.44	0.67
Series 13	26	0.87	3.66	0.61
Series 15a	18	0.60	14.48	1.24
Series 15b	14	0.47	11.76	0.84
Series 18	10	0.33	8.21	0.70
Series 19	16	0.53	10.44	1.74
Mean	21.5	0.72	13.04	1.66

where A^m is the falcon's metric size and a^p the pixel size in the original image.

(6) The average relative velocity (just velocity from now on) across the event was computed as

$$< V > = L^m/\Delta t. \quad (2)$$

Table 1 reports relative velocities for 15 wave pulses, again selected for their high optical quality. The uncertainties associated with such measurements vary from 7% to 17%. The case in which the travelling wave changes its distance with respect to the observer is discussed in the Appendix. In such a scenario, errors on velocities can be even greater, but velocity itself is always underestimated. So we can state that lower limits to velocities are determined with a precision varying from 7% to 17%.

RESULTS AND DISCUSSION

Our observations suggest that WEs represent an antipredator behaviour. In agreement with similar studies in other species of insects and fish (Webb 1980; Treherne & Foster 1981; Gerlotto et al. 2006, Kastberger et al. 2008), we found that WEs occurred almost exclusively under predator threat: observed exceptions, elicited by helicopters or gulls, are still to be considered as antipredator reactions. We studied 329 hunting sequences (HSs), 210 of which triggered WEs.

WEs showed up at least once on 77% of all observation days and in 42% of HSs (0.66 times per HS). WEs were homogeneously distributed across the study period (December–March) divided into five blocks of 2 weeks ($\chi^2_4 = 4.5$, $P = 0.34$). In one of the roosts there was a nonsignificant trend for WEs to increase during the season ($\chi^2_4 = 7.95, P = 0.09$). Importantly, WEs were more frequent and more likely to occur during unsuccessful hunting sequences (Mann–Whitney test: $z = 2.351$, $N_{successful} = 52$, $N_{unsuccessful} = 165$, one-tailed $P = 0.019$; Fisher's exact test comparing HSs with or without WEs: two-tailed $P = 0.009$), as the success rate of predation in the presence of WEs was 0.14 and in the absence of WEs 0.30 (Table 2).

This result suggests an antipredator effect for WEs and shows that waves form only under specific circumstances. Moreover, by direct observation, we could exclude the possibility that environmental or weather conditions (such as wind or rain) can affect WEs. One possible hypothesis is that flock responses depend on the hunting strategies adopted by falcons (Rudebeck 1951; Zoratto et al. 2010), to maximize the probability of escaping an attack, as suggested by the predator–prey coevolution theory (Dawkins & Krebs 1979). That wave formation and dynamics can depend on the predator's behaviour has been demonstrated in giant honeybees, *Apis dorsata*, in response to hornets, *Vespa* sp. Their waves are modulated in strength and rate by the predator's speed and proximity (Kastberger et al. 2008).

Table 2
Predation success in relation to wave occurrence for all hunting sequences

Predation	No wave	Wave	Total
Unsuccessful	97	68	165
Successful	41	11	52
Total	138	79	217

Referring to the position of the falcon with respect to the flock, we grouped the attacking directions into 'above', 'below' and 'lateral' in all HSs for which we had information on attack direction ($N = 175$ sequences): on average falcons preferred to attack laterally and there were more attacks from above than from below ($F_{2,\ 348} = 32.6$, $P < 0.0001$; Fig. 2a). Furthermore, waves were observed propagating downwards more than upwards and

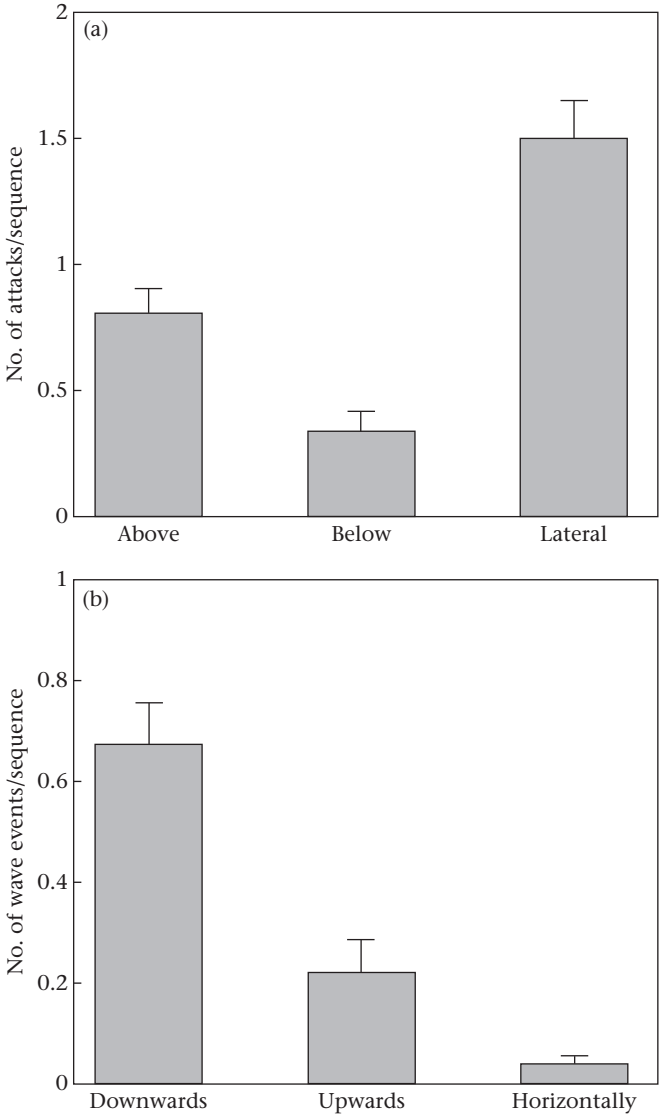

Figure 2. (a) Direction of attack: number of attacks per sequence (mean + SEM) from the three directions with respect to the flock (above, below and lateral). (b) Direction of wave propagation: number of waves (mean + SEM) propagating in the three directions within the flock (downwards, upwards and horizontally) in a hunting sequence.

upwards more than horizontally ($F_{2,\ 348} = 34.0$, $P < 0.0001$; Fig. 2b, see also Appendix Table A2), hinting at some unknown mechanism inhibiting wave formation when the attack came from the predator's preferred direction. However, we noticed that flocks that failed to produce WEs tended to be sparser than those that produced them, suggesting that there could be a sort of threshold, in density or cohesion, for waves to originate and propagate. Unfortunately, we were technically unable to quantify density in our flocks, so this remains an anecdotal observation to be further evaluated. A critical density has recently been shown to trigger the formation of vast fish shoals of millions of individuals, independently from predators (Makris et al. 2009).

Systematically, waves formed in proximity to the falcon (Fig. 3) and propagated away from it (Appendix Table A2), thus excluding any mobbing function as hypothesized in the Introduction. On the contrary, these results suggest that the predator is the perturbation physically giving rise to the propagating wave. The fact that the wave initiation is near the source of an attack is known for bird flocks (although not explicitly called waves) and fish schools only under simulated attack (Radakov 1973; Potts 1984). Here, we have characterized this phenomenon under true predation. Earlier literature (Heppner 1997) suggested that waves, in birds, could be associated with an antipredator context. Our study shows that WEs result from a collective escape attempt.

WEs could last several seconds (in 21 WEs, selected from our data set, up to 19.2 s for 20 pulses) and the frequency of pulse emission had a distribution with a marked peak around its average value, about 1.3 per s (Appendix Table A1). Conversely, the distribution of wave velocity was broader (ranging from 3.7 m/s to 25.2 m/s, Table 1) with a large inter- and intraflock variability. Moreover, wave velocity was often greater than the absolute velocity of the flock (Table 1; Ballerini et al. 2008a), a property that seems general and applies to similar phenomena of collective behaviour in other species (Radakov 1973; Davis 1980; Potts 1984; Axelsen et al. 2001; Gerlotto et al. 2006). This result is consistent with the 'Trafalgar effect' whose major feature is that the velocity of propagation of the perturbation inside the group is greater than the velocity of the individual (Treherne & Foster 1981; Gerlotto et al. 2006). No correlation between the flock–falcon distance (D_{FF}) and velocity was observed. As for elastic waves, the velocity of the perturbation did not seem to depend on the intensity of the perturbation itself (i.e. D_{FF}). Since, in elastic waves, this velocity depends exclusively on the inner structure of the medium, we believe that, analogously, in starling flocks, wave velocity depends on cohesion and density.

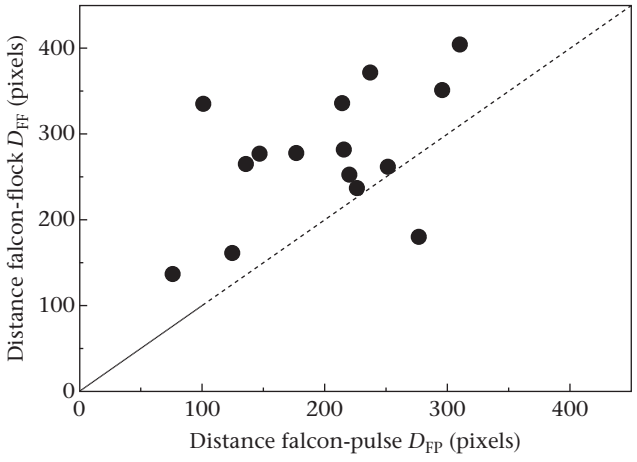

Figure 3. Origin of waves: pixel distance between the falcon and the centre of the flock, D_{FF}, versus the distance between the falcon and the centre of the pulse, D_{FP}, at the initial time of 15 independent WEs. These WEs involved only one, easily traceable, falcon. Typically $D_{FP} < D_{FF}$.

This study is an attempt at quantifying wave collective behaviour in flocks of thousands of individuals. That density is a key quantity in determining the dynamics appears from nearly all the issues addressed here. Mechanically, the falcon acts as a perturbation of the resting state of those starlings that manage to discern it, typically those on a specific part of the surface of the flock. Each one reacts by trying to escape from the predator: sometimes a single flock under attack was observed to split in two, even with waves propagating in both parts. If starlings are free to move, they flee and no wave occurs. Still, at short mutual distances, their flight is constrained by their neighbours: to avoid collisions, the interindividual distance is reduced until a certain limit is reached. Thus a deformation follows the perturbation, producing fluctuations in density on timescales related to the avoidance mechanism. For this reason, our guess is that wave velocity may depend on the strength of the repulsive forces between individuals at short distances. Our observations also do not exclude a similarity with a human chorus line as suggested for dunlin flocks (Potts 1984). Despite some recent insight into interindividual interactions in bird flocks (Ballerini et al. 2008b), much remains to be understood and future research in individual-based modelling of collective animal behaviour could benefit from our empirical data (Hildenbrandt et al. 2010; Hemelrijk & Hildenbrandt 2011).

WEs are a straightforward example of emerging complexity: a simple functional response (escaping from predators), when affecting even just a relatively small portion of a cohesive flock of thousands of individuals, can produce very complex patterns. Probably, in birds, WEs occur only when the perturbation is so strong that individuals almost come into contact, which is probably the reason why they form only in the presence of a threat. WEs possess a measurable antipredator function: it is likely that rapid variations, in local density and in both predator–prey and prey–prey distances, perturb the visual perception of falcons. As suggested for similar phenomena (e.g. Trafalgar wave) in giant honeybees (Kastberger et al. 2008; Schmelzer & Kastberger 2009), dunlins (Buchanan et al. 1988) and marine insects (Treherne & Foster 1981), we found that, also in starlings, waves can hamper predation success.

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Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.07.006.

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APPENDIX

Sources of experimental error

Parallax error

Equation (1) in the main text ($L^{\mathrm{m}} = L^{\mathrm{p}} \times A^{\mathrm{m}}/a^{\mathrm{p}}$) is a good estimator of the metric distance L^{m} assuming that the falcon and the flock are approximately at the same distance (depth) from the video camera, but since our approach is not stereoscopic (Ballerini et al. 2008a) it is not possible to verify this. To quantify in our case how accurate this approximation is, we proceed in the following way.

Let us suppose first that the trajectory of the wave front in the real space, $\boldsymbol{l}^{\mathbf{m}}(t)$, lies on a plane p approximately perpendicular to the optical axis of the camera (z direction), while the falcon is out of the plane, with a displacement dz along the axis direction.

For a conservative estimate of dz, one can imagine that dz is approximately of the same magnitude as the distance between falcon and flock on the image plane, which can be expressed as:

$$dz \sim \|\boldsymbol{l}^{\mathbf{m}}(0) - \boldsymbol{f}(0)\|,$$

where $\boldsymbol{l}^{\mathbf{m}}(0)$ and $\boldsymbol{f}(0)$ are the initial positions of the wave front and the falcon.

According to optics, the error on L^{m} induced by the previous scenario amounts to:

$$dL^{\mathrm{m}}/L^{\mathrm{m}} = dz/z \sim \|\boldsymbol{l}^{\mathbf{m}}(0) - \boldsymbol{f}(0)\|/z \qquad \text{(A1)}$$

For our videos, all taken from the same location, z is always more than 200 m. To obtain an estimate of the numerator of the right-hand side of equation (A1), one can compute the distance in pixels between the initial positions of the wave front and the falcon and then convert it into a metric distance by use of equation (1), which gives a first approximation value. From our data, for 15 WEs this distance varies from 5 to 19 m (average about 12 m). Taking all these values into account, we finally get an average relative error due to parallax effects of

$$\mathrm{d}z/z < 5\%,$$

which is negligible in most WEs (see below). Moreover, it is an overestimate of the actual error, since the attacking predator's orientation, which is clear from its bill–tail asymmetry, is most of the time nearly perpendicular to the optical axis.

Let us now consider the complementary situation, where falcon and pulse are on a plane p perpendicular to the optical axis at the initial time ($t = t_{\mathrm{in}}$), but the pulse trajectory leaves the plane at subsequent times. In this case, one would not track the trajectory $\boldsymbol{l}^{\mathbf{m}}(t)$ itself but rather its projection on p, $\boldsymbol{l}_p^{\mathbf{m}}(t)$. One can imagine that the real trajectory runs in the z direction for as much as it runs on p, which is a rather conservative approximation. Namely

$$\int_{t_{\mathrm{in}}}^{t_{\mathrm{fin}}} \left\| \frac{d\boldsymbol{l}_p^{\mathbf{m}}(t)}{dt} \right\| dt$$

Then the length L^{m} of the trajectory is, by the Pythagorean theorem,

$$\sqrt{2} \int_{t_{\mathrm{in}}}^{t_{\mathrm{fin}}} \left\| \frac{d\boldsymbol{l}_p^{\mathbf{m}}(t)}{dt} \right\| dt,$$

which results in a correction of approximately 40% of the original value.

We note that with the procedure that we followed, we are always underestimating L^{m}, so that the computed velocities of the wave pulses are lower limits to the real velocity values. The uncertainties that are associated with velocities in the Results and discussion section refer to such lower boundaries. As a consequence, real velocities of waves can be up to 40% bigger than their associated lower limit. Unfortunately, there is no means to judge the 3D structure of our flocks and, as we report in the Results and discussion section, waves follow the morphology of the flock, its shape and borders. So our results consist of window intervals

where, as far as we know, true velocities fall with a uniform distribution, but whose boundaries are very well estimated.

Besides, as we selected those WEs that were more clearly visible in the camera's ccd reference frame, it is likely that they correspond to waves propagating with a very large projection perpendicular to the optical axis, so that 40% of uncertainty is a highly overestimated value, the lower limit itself being a good approximation of the real velocity.

Errors from the parameters of *equations (1) and (2)*

Once the validity of equation (1) is established, the errors derived from its parameters can be calculated. Such analysis must be carried out case by case, but we present here a general discussion of how we proceeded.

L^{p}, the length in pixels of the trajectory, depends on four parameters, two thresholds (T_{F} and T_{P}) and two Gaussian parameters (mean and SD of the Gaussian curve defining the Gaussian-splined trajectory). The last two are fixed by the choice of this Gaussian curve.

Besides, it turns out that L^{p} is very sensitive to T_{P} but very stable with respect to T_{F}.

In particular, considering $L^{\mathrm{p}}(T_{\mathrm{P}})$ one can observe, for all the events, a plateau for L^{p} corresponding to a certain interval I in T_{P}. Beyond the extremes of I, L^{p} varies abruptly while inside it is very stable, so the final value of L^{p} is obtained as an average:

$$L^{\mathrm{p}} = \frac{1}{I}\int_{I} L^{\mathrm{p}}(T_{\mathrm{P}})\, dT_{\mathrm{P}}.$$

The experimental error due to such indeterminacy of T_{P} over the interval I is negligible ($dL^{\mathrm{m}}/L^{\mathrm{m}} \sim 1\%$).

a^{p} also is a minor source of error, since we know the size of the falcon with the resolution of half a pixel and then take the average across the frames involved in the WE ($dL^{\mathrm{m}}/L^{\mathrm{m}} < 4\%$).

The major source of error in equation (2) is likely to be the result of the determination of A^{m}.

From the literature, we know a range of both length and wing span for males and females (Cramp & Perrins 1994). An error may come from the fact that individual differences between falcons could affect our measurement (females are about 15% larger than males), and we could not distinguish the sex. Our images usually presented the predator flying parallel to the image plane, so it was possible to use the average body length (42 cm), assumed to be less variable than the wing span (falcons soaring with their wings extended to the maximal span are hardly ever observed, since this is not a common behaviour during hunting). Furthermore, we have three events in which the falcon was slightly deflected from the direction parallel to the image plane. In these instances we assigned a different value (60 cm).

Given the variability in body length and wing span (36–48 and 95–110 cm, respectively) and assuming a Gaussian distribution for structural morphometrics (S. Casagrande, unpublished data on tarsus measurements in the kestrel, Falco tinnunculus, Italian population, a similar falcon species), we obtain

$$7\% < dL^{\mathrm{m}}/L^{\mathrm{m}} < 17\%$$

which in most cases represents the most relevant contribution to velocity uncertainties.

A last source of uncertainty in both frequency and velocity measurements is the identification of the temporal interval Δt. Having 30 frames/s makes our time measurements very accurate, so that velocity resolution is completely unaffected by the uncertainty in Δt. When calculating the average frequencies of the wave emission during the same train, we can easily establish the number of fronts running inside the flock without errors. One can be uncertain about the exact initial and final frames of the train, so that the errors for frequencies are due only to an uncertainty of 1/30 s for Δt.

Table A1
Frequency of single wave pulses in each of 21 wave events

Wave event	Frames	Duration (s)	Count	Frequency (per s)	Error (per s)
Series 1c	90	3.00	6	2.00	0.02
Series 1d	119	3.97	5	1.26	0.01
Series 4	80	2.67	4	1.50	0.19
Series 8abcd	575	19.20	20	1.04	0.00
Series 9	89	2.97	4	1.35	0.02
Series 10	119	3.97	2	0.50	0.00
Series 12	135	4.50	5	1.11	0.01
Series 13	153	5.10	4	0.78	0.01
Series 14	99	3.30	5	1.51	0.01
Series 15a	71	2.37	7	2.95	0.04
Series 16	103	3.43	4	1.17	0.01
Series 2	93	3.10	4	1.29	0.01
Series 6a	169	5.63	4	0.71	0.00
Series 6b	140	4.67	6	1.28	0.01
Series 17	90	3.00	3	1.00	0.01
Series 18	95	3.17	4	1.26	0.01
Series 19	66	2.20	2	0.91	0.01
Series 19b	90	3.00	3	1.00	0.01
Series 22	60	2.00	3	1.50	0.02
Series 23	125	4.17	5	1.20	0.01
Series 24	66	2.20	3	1.36	0.02
Mean	125	4.17		1.27	0.10

Table A2
Wave events observed and their directions of propagation with respect to the position of the falcon

Direction with respect to falcon	Wave events
Downward escaping	142
Upward escaping	38
Downward towards falcon	0
Upward towards falcon	0
Horizontal escaping	9
Horizontal towards falcon	0
Oblique downward escaping	12
Oblique upward escaping	9
Oblique downward towards falcon	0
Oblique upward towards falcon	0